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# FURTHER OBSERVATIONS ON BEES WHICH TAKE POLLEN FROM PLANTS OF THE GENUS SOLANUM

(Hymenoptera: Apoidea)
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Introduction. Two of the most common species of Solanum in the southwestern United States are S. elaeagnifolium Linnaeus and S. rostratum Dunal. The former (fig. 1) is known as silverleafnettle, bullnettle and Trompillo, and is a perennial species with purple flowers. The latter (fig. 2) is known as buffalo-bur and is an annual species with yellow flowers. Both are low-growing plants with prickly stems, which are especially notable in S. rostratum. Each makes its pollen available shortly after dawn as the buds begin to open and each is pollinated, insofar as presently known, primarly by large, heavy-bodied bees which are capable of inverting the flowers and vibrating the anthers in order to extract the pollen from the slits at their ends. Smaller bees are able to exploit residual pollen in the face of competition from the larger bees but the principal harvest is reaped by the latter—at least in the areas where our studies have been conducted.

Although the leaves and unripe fruit of *S. rostratum* and *S. elaeagnifolium* are reported to contain an alkaloid, solanin, highly toxic to vertebrates, there is no indication of toxicity of the pollen to bees—nor, for that matter of the leaves to the Colorado potato beetle, which feeds readily on *S. rostratum*, its presumed original host plant.

Previous Studies. Some observations on the activity of pollinators of Solanum elaeagnifolium have been reported previously for a small group of plants on the grounds of the Southwestern Research Station, 5 miles west of Portal, Arizona (Linsley, 1962). This site is at an elevation of 5400 ft. in the Chiricahua Mountains, and during the last week of July, the flowers began to open near 5 a.m., at which time the first pollinators appear. Air tempera-

<sup>&</sup>lt;sup>1</sup> The photographs accompanying this paper were very kindly taken for this purpose by Marjorie Statham of the American Museum of Natural History, New York. Miss Statham and Juanita M. Linsley ably assisted in the collection of field samples. Identifications of pollinators were made or confirmed by P. H. Timberlake, University of California, Riverside, of plants by Margaret S. Bergseng, University of California Herbarium, Berkeley. Robbin Thorp, Department of Entomology and Parasitology, University of California, Berkeley, aided in the identification and analysis of pollen loads and comparison of pollen-collecting structures. The authors are grateful to all concerned.

tures at this hour were in the vicinity of 56°-58° F, well above the minimum necessary for flight. The first active pollinators were *Ptiloglossa arizonensis* Timberlake, followed by *Bombus morrisoni* Cresson and *B. sonorus* Say, from 10 minutes to half an hour later. These were the only pollinators observed in this area, the *Ptiloglossa* females confining their activity largely to a 15 or 20 minute period which terminated considerably before sunrise, the *Bombus* continuing to work the flowers until they began to wilt (near midmorning on a hot day, near mid-day when the sky was overcast). No similar data have been published for bees which take pollen from *Solanum rostratum*, although P. H. Timberlake found *Protoxaea gloriosa* (Fox), *Psaenythia mexicanorum* (Cockerell) and *Nomia tetrazonata* Cockerell visiting this plant at Sonoita Creek, near Patagonia, Santa Cruz County, Arizona.

Site of Present Study. In the summer of 1962, at a location one mile east of Douglas, Cochise County, Arizona, populations of both species of Solanum were in bloom and growing adjacent to one another. S. rostratum occurred as individual plants or in small groups of plants in a narrow wash dominated by the tall composite, Verbesina enceliodes (Car.) Benth. & Hook., var. exauriculata R. &. G. S. elaeagnifolium occurred in thin scattered patches on somewhat higher ground extending eastward from the wash, and was associated with Hoffmanseggia densifora Benth., Baileya multiradiata Harv. & Gray, Bahia absinthifolia var. dealbata Gray, Mentzelia pumila (Nutt.) Torr. & Gray, Cucurbita foetidissima H.B.K., C. digitata Gray, and a number of less conspicuous flowering plants. Scattered shrubs of Larrea tridentata (D.C.) Coville, and other desert perennials characterized the surrounding area. The physical proximity of individual plants of the two species of Solanum greatly facilitated a comparison of the pollinators which visited them. Further, the sound emitted by the bees while vibrating the anthers could be heard at a distance of several yards, a fact which contributed materially to the ease with which they could be located in the dim morning light.

Size, appearance, and geographical range of the pollinators. The most conspicuous of the Solanum pollinators is the bumblebee Bombus sonorus (figs. 3-5), the workers of which are large (our samples varying in length from 13-18 mm), robust, densely hairy, and black, with the pubescence of the dorsum of the thorax bright yellow, broken with a transverse black band across the middle,



 $Fig.\ 1.\ Solanum\ elaeagnifolium\ Linnaeus.$ 

and that of the first three metasomal terga bright yellow also. It occurs in Mexico and southwestern United States from Texas to southern California and northward to Kansas. Caupolicana yarrowi (figs. 3-5) is also large (17-19 mm in length), robust, black, and densely hairy, the hairs of the face mostly white, those of the vertex of the head and dorsum of the thorax fulvous, and the metasoma transversely banded with white along apical margins of first four terga. It also occurs in Mexico, extending its range into southern Arizona, New Mexico and Texas. Ptiloglossa jonesi (figs. 3-5) is similar in size (16-19 mm) and the hairs of the face and dorsum of the thorax are similar, but the metasoma is greenish with the apical margins of the terga paler, superficially suggesting transverse pubescent bands. Thus far it is known only from southern Arizona and northern Mexico. Protoxaea gloriosa (figs. 3-5) is likewise similar in size to the preceding (15-18 mm in length), and is a robust black bee with reddish legs. The facial pubescence is mostly white, that of the vertex of the head, dorsum of the thorax, and the base, sides and apex of the metasoma fulvous. We have seen examples from Mexico, Texas, and New Mexico, as well as Arizona. All three species of Centris are robust, black bees with white facial hairs, and the pubescence of the vertex, dorsum of thorax, and base of metasoma fulvous. However, C. caesalpiniae (figs. 5, 6) has red eyes and a red clypeus and has about the same size range as Protoxaea (14-18 mm in length), and occurs in much the same area. C. atripes (fig. 6) is intermediate in size (10-14 mm in length) and has a bright yellow clypeus and labrum. It is known from northern Mexico, Texas, New Mexico and Arizona. The similar sized C. rhodopus (fig. 6) (11-13 mm in length) has the base of the antennae, eyes, clypeus, mouthparts and legs wholly or partially red. It overlaps the other two species in distribution but also occurs in southern California. Psaenythia mexicanorum (figs. 5, 6) and Nomia mesillensis depart from this pattern of large, robust, hairy bees with dense fulvous thoracic pubescence. (They range from 9-10 mm in length). The former is black with the lower face largely bright yellow and with transverse white pubescent bands at the base of metasomal terga, two to four; the latter has gold maculations with greenish tints apically on metasomal segments two to four. Both are southwestern species which extend their range into Mexico.

Nature of the pollen. The pollen of each of the species of So-

lanum is very fine, the equatorial diameter of the grains in our sample from S. rostratum ranging from  $23-27\mu$ , those from S. elaeagnifolium, from  $32-37\mu$ . As in other species of Solanum, pollen is shed from slits in the end of the five elongate anthers



Fig. 2. Solanum rostratum Dunal.

which surround the exerted stigma. The weight of the larger bees causes the flowers to invert as they alight, and the anthers are then vibrated and the pollen shaken out. In this process the venter of the bee often becomes covered with pollen, in addition to that which is packed into the specialized hairs which constitute the pollen-carrying scopa.

We have called attention previously (Linsley, 1962), to the high proportion of "aborted" pollen grains produced by Solanum elaeagnifolium. In samples taken from bees in the Chiricahua Mountains, in 1961, 64 per cent of the pollen grains were aborted (i.e., did not contain significant amounts of protoplasm). Samples from the Douglas site were almost identical (65.4 per cent), suggesting that the percentage of aborted grains is the result of some inherent factor, rather than a function of temperature as suggested by Stow (1927). S. rostratum produces aborted pollen also, but at Douglas, where the plants were intermixed with those of S. elaeagnifolium, the proportion of aborted grains was only 15.6 per cent.

Among the plant species which compete for the attention of some of the Solanum pollinators, Mentzelia pumila also produces fine pollen, with grains varying in diameter from  $25-27\mu$ , much as in Solanum rostratum. Its pollen is made available in the late afternoon and early evening, and is exploited at that time by Bombus, Caupolicana, and Centris, but not by Ptiloglossa or Protoxaea. On the other hand, Hoffmanseggia densifora produces a much coarser pollen, our samples ranging in diameter from 61- $74\mu$ . It is utilized during the day by the Solanum species of Centris, but not by Ptiloglossa, Caupolicana, or Protoxaea.

Devices for the collection and transport of pollen. In view of the small size of the pollen grains produced by the two species of Solanum, a brief comparison of the nature of the specialized devices for pollen-holding (scopae) present in the various species may be of interest.

Bombus sonorus, like other social bees, collects pollen in a corbicula consisting of a large, slightly concave, smooth, glabrous area on the outer surface of each of the posterior tibiae. The tibiae are wide and flattened, and the corbiculae are surrounded anteriorly and posteriorly by long, incurved, stiff black hairs which hold the moist pollen mass which is formed by mixing nectar with the pollen to provide consistency. At the inner distal end of each

of the posterior tibiae there is a "rake" (rastellum) formed of short, stiff setae. The outer surface of the posterior basitarsi has a flattened "auricle" which functions to push pollen upward into the corbicula. The inner surface of the basitarsi has rows of stiff setae forming comb-like structures.

Ptiloglossa jonesi and Caupolicana yarrowi are essentially similar in the nature of the specialized pollen collecting hairs which are present on the trochanters, femora, tibiae and basitarsi of the hind legs and on the sides of the propodeum and first metasomal tergum. Except on the hind basitarsi, scopal hairs are long, white, and dense, with whorled branches. Those of the trochanters curl

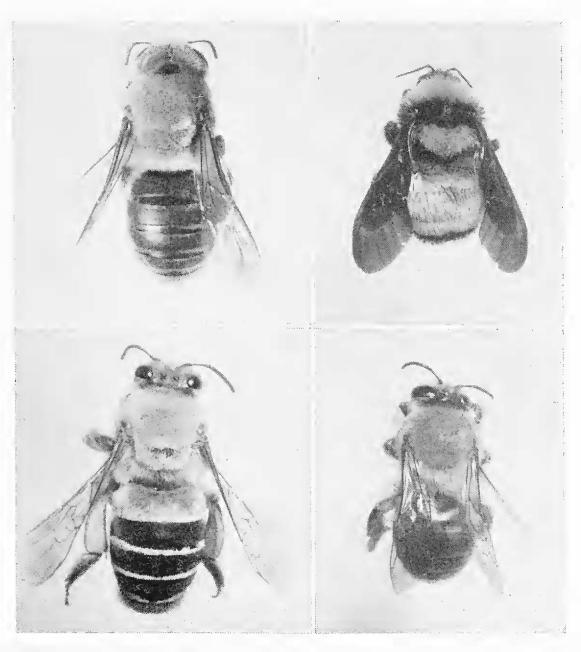


Fig. 3. Solanum pollinators, dorsal view. Upper left: Protoxaea gloriosa (Fox). Upper right: Bombus sonorus Say. Lower left: Caupolicana yarrowi (Cresson). Lower right: Ptiloglossa jonesi Timberlake.

ventrally and apically; those of the femora, ventrally; those of tibiae, ventrally and apically; those of the lateral face of the propodeum, posteriorly and ventrally; and those of the first metasomal tergite, ventrally. The hairs of the inner face of the hind tibiae, and the mid and hind basitarsi, are shorter, moderately dense, dark, simple, stiff, and directed ventrally. The pollen is packed dry.

Protoxaea gloriosa carries pollen in specialized scopal hairs on the posterior coxae, trochanters, femora, the anterior surface of posterior tibiae and dorsal one-fourth of anterior surface of posterior basitarsi, and the sides of the propodeum and first metasomal tergum, as well as the middle of the first metasomal sternum. The scopal hairs are long, pale yellow brown, dense, somewhat curved, with whorled branches. The hairs of the coxae are curled apically and become shorter toward the base; those of the trochanter are curled apically; those of the femora, ventrally and apically. Hairs of dorsal surface of tibiae and dorsal one-fourth of anterior surface of hind basitarsi, shorter, straight, and directed apically, those of ventral surface, longer, curled ventrally and somewhat apically. On the inner faces of the posterior legs, the hairs are very like those of Ptiloglossa jonesi and Caupolicana yarrowi. On the lateral face of the propodeum the scopal hairs are directed posteriorly and ventrally, on the sides of the first metasomal segment, ventrally, and on the middle of the first metasomal sternum, posteriorly. The pollen is packed dry.

Centris caesalpiniae, C. atripes, and C. rhodopus have essentially similar pollen collecting devices. The scopa is confined to the outer surface of the posterior tibiae and basitarsi, and is composed of dense, long, stiff, black hairs, both branched and simple. The two types of hairs appear to alternate and are represented in about equal numbers. The simple hairs are slightly longer and when the scopa is packed full of pollen, these may be the only hairs visible. The branches of the plumose hairs consist of two lateral rows on apical half of hair, and they do not subdivide further. The hairs of the inner surface of the posterior tibiae are short and simple, those of the inner surface of the posterior basitarsi are also simple, but longer, although not as long as those of outer surface. The pollen is presumably packed dry, although on several specimens it appears damp and matted, as though small amounts of nectar might be present.

In Psaenythia mexicanorum the scopa is confined to the pos-

terior tibiae, which are long and narrow with the outer surface flattened. The hairs which comprise it are short, white, sparse and curved posteriorly. Those on the apical half of the tibiae are branched on the outer side. The anterior half of the inner surface of the posterior and mid basitarsi have dense, stiff, yellowish, simple hairs. The pollen is mixed with nectar and packed into the scopa moist.

Nomia mesillensis carries pollen in scopal hairs on the outer surface of the posterior tibiae, the inner surface of the posterior femora, the posterior trochanters, and on the side of the propodeum. Some pollen is also carried on the base of the posterior basitarsi and the apices of the abdominal sterna.

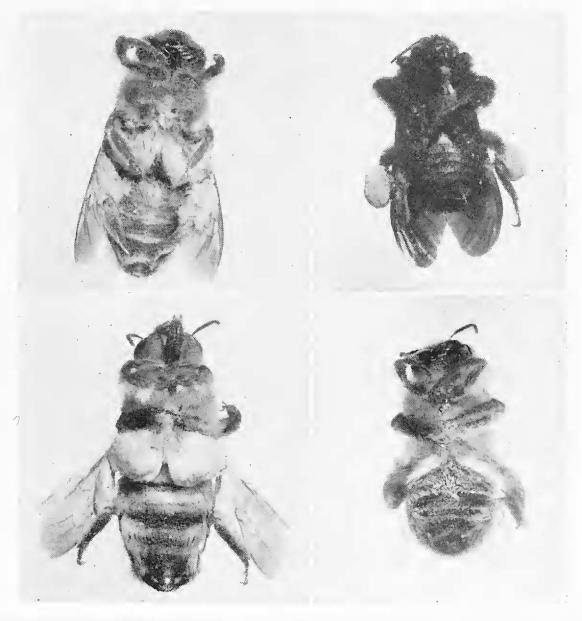


Fig. 4. Solanum pollinators, ventral view. Upper left: Protoxaea gloriosa. Upper right: Bombus sonorus. Lower left: Caupolicana yarrowi. Lower right: Ptiloglossa jonesi.

Constancy among the pollinators. All of the individuals of Ptiloglossa jonesi had pure loads of Solanum pollen except two individuals which, when they arrived at dawn, carried tricolporate grains from an unknown plant species on the legs, and two which carried pollens superficially resembling that of Solanum but probably different. On the other hand, nearly 70 per cent of the females of Caupolicana yarrowi already carried small to large quantities of an unidentified Mentzelia-like pollen when they began collecting from Solanum. Caupolicana collects pollen from Mentzelia pumila in the evening but the flowers of this plant are closed in the morning. Matinal activity of Caupolicana yarrowi has been recorded about flowers of Datura (Cockerell and Porter, 1899), Larrea (Linsley and Hurd, 1959) and Melilotus (Linsley, 1960), but except for the general statement of Michener (1961) that the species is not oligolectic, we have been unable to find direct or indirect references to its pollen-collecting activity.

All Psaenythia mexicanorum which were carrying pollen had pure loads; the remainder were parasitized and made no athempt to gather pollen. We have found this species taking nectar from Verbesina but have not observed it collecting pollen from any plants but Solanum. Bombus sonorus, a polylectic species, was remarkably constant when visiting Solanum; of 131 individuals examined, approximately 85 per cent had pure loads. Among the remainder, some of the early arrivals carried the unknown Mentzelia-like pollen or pollen believed to have been derived from some member of the Liliaceae; a few of the late arrivals had some pollen from Compositae probably Verbesina encelioides. Protoxaea gloriosa, another polylege, had a high proportion of mixed loads (approximately 53 per cent), the foundation of the loads having been derived from the undetermined plant with Mentzelia-like pollen. It is known to take pollen also from Kallstroemia californica (Linsley and Michener, 1962).

Of the three species of Centris, C. caesalpiniae exhibited the greatest amount of constancy (approximately 59 per cent), followed by C. atripes (37 per cent) and C. rhodopus (16 per cent). The mixed loads in all three species mostly involved pollen from Hoffmanseggia densiflora, or the unidentified plant with Mentzelialike pollen, or both. Snelling (1956), in his synopsis of the taxonomy, distribution and flower records of the nine species of Centris which are known to occur within or extend their ranges

into California, lists none as visiting Solanum. Nor does he give pollen sources for either C. atripes nor C. rhodopus. We have found the latter taking pollen from Dalea spinosa, and all three of the Solanum-visiting species taking nectar from Verbesina encelioides, in addition to the other pollen and nectar sources listed herein.



Fig. 5. Solanum pollinators, lateral view. Upper left: Caupolicana yarrowi. Upper right: Psaenythia mexicanorum. Center left: Centris caesalpiniae. Center right: Bombus sonorus. Lower left: Protoxaea gloriosa. Lower right: Ptiloglossa jonesi.

It is of interest that all of the large matinal pollinators of Solanum except Ptiloglossa jonesi and Protoxaea gloriosa also exploit the fine pollen grains of Mentzelia, when they are offered in the late afternoon. On August 20, for example, about two hours before sunset, many of the Mentzelia flowers were opening and were being visited by Bombus at 4:45 p.m. (air temp. 90° F). An hour before sunset, at 5:50 p.m., the first female Caupolicana was observed taking pollen, the last, 22 minutes after sunset², at 7:13 p.m. (air temp. 81° F); the first Centris was seen 17 minutes before sunset, at 6:34 p.m., the last, 16 minutes after sunset, at 7:07 p.m.; and the last Bombus at 7:02 p.m. No Ptiloglossa or Protoxaea were observed at Mentzelia on this evening nor any of the numerous others when Mentzelia samples were taken. Examination of the pollen loads of the individuals visiting Mentzelia revealed only pure Mentzelia pollen.

Effects of Physical Factors on Pollinator Activity. During the entire period in which observations were made of pollinator activity, the air temperatures were well above levels at which they might be expected to limit flight. The only behavioral variation noted that might have been influenced by differences in temperature was that the amount of time spent extracting pollen from a flower varied from 2.5-3 seconds at 68-72° F. to from 1-2 seconds at 80-84° F., for both Ptiloglossa and Caupolicana. Other species were not checked on this point.

The most critical factor noted by us was variation in light intensity, and particularly direct radiation from the sun. On clear warm mornings such as August 17 (Table I), Ptiloglossa and Caupolicana begin collecting pollen from both species of Solanum about an hour before sunrise, although they can be heard in exploratory or orientation flights somewhat earlier—usually at considerable distance above our heads. The first Bombus usually appear about 20 minutes later, and although Ptiloglossa and Caupolicana cease pollen collecting an hour or less after sunrise, Bombus continue until the flowers wilt in late morning. Occasional individuals of Protoxaea are active at flowers before sunrise, but the main period of pollen-collecting begins at sunrise and continues for from two to two and one-half hours. Pollen-gathering by Centris also begins at sunrise and reaches a peak about two

<sup>&</sup>lt;sup>2</sup> Caupolicana females start flying at dawn and were active at flowers of Solanum almost an hour before sunrise at a much lower light intensity than that which prevails when they cease flight in the evening.

hours later. *Psaenythia* do not appear in numbers until midmorning when the pollen supply is running low. At this time they are joined by *Nomia*.



Fig. 6. Solanum pollinators. Upper left and right: Psaenythia mexicanorum (Cockerell). Center left: Centris rhodopus Cockerell. Center right: Centris atripes Mocsary. Lower left and right: Centris caesalpiniae Cockerell.

Table I. Pollen-collecting bees at plants of two species of Solanum at a site one mile east of Douglas, Arizona, August 17, Sunrise: 6:00 a.m. MST. 73° F +0 QO° F 1969 under clear sk

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Table II. Pollen-collecting bees at plants of two species of *Solanum* growing together one mile east of Douglas, Arizona, August 18, 1962, under overcast sky from 5 to 7 a.m. and broken sky thereafter, with temperatures ranging from 64.3° F. to 86.3° F. Sunrise (behind clouds): 6:03 a.m.

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By contrast, on overcast mornings such as that of August 18 (Table II), the active period of pollen collecting for *Ptiloglossa* extends over a period of two and one-half hours, that of *Caupolicana* over three and one-half hours. *Protoxaea* initiates activity about an hour later than usual but terminates pollen collecting at about the same time as on a clear day. *Centris* spp. behave about the same as *Protoxaea*. On this particular day *Psaenythia* appeared somewhat earlier than usual but in numbers too small to judge whether or not this had any significance.

#### Summary

- (1) Flowers of  $Solanum\ elaeagnifolium\ and\ S.\ rostratum\ open$  and expose the anthers shortly after dawn.
- (2) The pollen is exploited primarily by large, heavy-bodied bees which invert the flower and vibrate the anthers, shaking pollen from slits in their ends.
- (3) When allowance is made for slight differences in the growing sites of the two species of *Solanum*, it is clear that the same species of bees visit both about equally.
- (4) Although individuals of some species appeared to be relatively pollen-species constant, others were seen to move from one *Solanum* to the other, in spite of the fact that to the human eye one is yellow, the other purple.
- (5) The polen grains are fine, ranging in the two species from  $23-37\mu$ , and the principal pollinators are clothed with fine hairs and modified pollen carrying devices which permit their exploitation.
- (6) Both *Solanum* species produce "aborted" pollen, amounting to about 65 per cent for *S. claeagnifolium*, nearly 16 per cent for *S. rostratum*.
- (7) Since "aborted" pollen grains lack protoplasm they presumably have no nutritional value for bee larvae.
- (8) The modified hairs are useful for carrying other kinds of fine pollen, such as that of *Mentzelia*, which is also exploited by some of the *Solanum* visitors when it is made available in the late afternoon near sunset.
- (9) The behavior pattern which results in vibration of the anthers of *Solanum* carries over to *Mentzelia*, where it is not obviously needed.
- (10) Although individuals of Bombus, Caupolicana, and Centris learn to exploit pollen of Solanum near sunrise and Mentzelia

near sunset, this does not appear to be true of *Ptiloglossa* nor of *Protoxaea*.

- (11) Restriction of pollen collecting activity to early morning hours (*Ptiloglossa* and to a lesser extent *Protoxaea*), or to early morning and late evening hours (*Caupolicana* and to a lesser extent *Centris* and *Bombus*) would appear to have obvious adaptive value in a desert environment.
- (12) Composition of the pollinator populations and time periods and activity sequences was remarkably uniform on successive days, varying only in response to different weather conditions.
- (13) Psaenythia and Nomia appear to be largely pollen scavengers, exploiting residual Solanum pollen after the main period of pollinator activity.
- (14) The larger pollinators exhibit a striking similarity in coloration of the pubescense of the head and thorax, although it is not clear as to whether this convergence is coincidental or results from a common selective force.

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## RECENT LITERATURE

BIOLOGICAL CHARACTERISTICS OF THE MUTILLID SUBGENUS PHOTOPSIS BLAKE AND THEIR SYSTEMATIC VALUES (*Hymenoptera*). By William E. Ferguson. University of California Publications in Entomology, Vol. 27, No. 1, pp. 1-92, 7 pls., 2 figs. in text. April 25, 1962. \$2.00.

A REVISIONAL STUDY OF THE BEES OF THE GENUS PERDITA F. SMITH, WITH SPECIAL REFERENCE TO THE FAUNA OF THE PACIFIC COAST. (Hymenoptera, Apoidea). Part V. By P. H. Timberlake. University of California Publications in Entomology, Vol. 28, No. 1, pp. 1-124, 13 pls., 2 figs. in text. April 30, 1962. \$2.50.—Pages 87-107 comprise a "Supplement to Parts I to IV." Included are descriptions of new species, new keys to the males of the subgenus *Macroteropsis* and to the females of the subgenus *Epimacrotera*, and a revision of couplets 19 to 26 in the key to the zonalis group of the subgenus *Perdita*.—H. B. Leech, California Academy of Sciences, San Francisco.

#### BOOK NOTICE

REVISION DES HYDROCANTHARES D'AFRIQUE (Coleoptera Dytiscoidea). By Félix Guignot. Annales du Musée Royal du Congo Belge, Sciences Zoologiques. Première partie, vol. 70, pp. 1-316, text figs. 1-293. January, 1959; price 260 francs. Deuxième partie, vol. 78, pp. 317-652, text figs. 294-572. December, 1959; 260 francs. Troisième partie, vol. 90, pp. 653-1000, text figs. 573-818. February, 1961; 230 francs. For sale by the Musée Royal de l'Afrique Centrale, Tervuren, Belgium.

This 3-volume monograph is essential for work on African hydrocantharids (Haliplidae, Hygrobiidae, Dytiscidae; the Gyrinidae have been treated elsewhere in detail by Brinck), and will have much wider use because of the keys and figures. There are a fair number of references to Nearctic species; most of these are in the footnotes—and of footnotes there are 844! There is a slip on p. 507 where the type species of the genus Hydrocanthus is cited as H. tricolor Say, a lapsus calami for H. iricolor Say, but there are remarkably few such errors. It is most unfortunate that Dr. Guignot did not live to see more than the first part of his work in print.—Hugh B. Leech, California Academy of Sciences, San Francisco.